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Department of Agricultural Biology [Zoology], University of Newcastle upon Tyne

Influence of *p*H, temperature and salinity on the fecundity and longevity of four species of Collembola

Barry R. Hutson[1])

With one figure

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Contents

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1. Introduction

Much work has been carried out on the role played by Collembola in litter breakdown and soil formation. This involves field studies of species composition, number, age structure, biomass, and respiration. The life history of Collembola under various environmental conditions must also be investigated in the laboratory. The experiments described here were undertaken during a survey of the fauna colonising reclaimed colliery waste sites in north-east England (Hutson 1974). Temperature, *p*H and salinity are three limiting factors encountered on reclamation sites and their effect on the fecundity and mortality of some collembolan species found on the sites was examined.

Very little work has been reported on the effects of *p*H on Collembola. From field surveys, many authors have not found any correlation between soil *p*H and population numbers, and have concluded that *p*H has little effect (Christiansen 1964). Gisin (1943), however, has shown *Odontella armata* (Axelson) to be typically basophil and *O. lamellifera* (Axelson) to be strictly acidophil. Maclagen (1932) showed in great detail that soil *p*H has a profound effect on the oviposition of *Sminthurus viridis* (L.). He found optimum oviposition at *p*H 6.5, and Davidson (1934) showed that a range from *p*H 5.5 to 7.0 is favourable for oviposition by this species. Ashraf (1969) found the fecundity of *Onychiurus bhattii* Yosii differed considerably with *p*H; after 14 days, the numbers of eggs laid by groups of 15 adults in soils of *p*H's 7.2, 7.5, 8.0, 8.5 and 9.7 were 295, 215, 79, nil and nil respectively. Most individuals survived except in the soil at *p*H 9.7.

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Data on individual species have often shown the influence of temperature on development, mortality and fecundity (SHARMA and KEVAN 1963a, b; CHOUDHURI 1960, 1963; HALE 1965a, b).

No references to the effect of salinity on Collembola have been found, which is, perhaps, to be expected since salinity levels are low and not a limiting factor in most agricultural soils. On colliery waste sites, however, salinity can be a major problem.

The species of Collembola used in this work were *Folsomia candida* (WILLEM) var. *distincta* (BAGNALL) which had been maintained in laboratory cultures for several years (referred to as **Lab.** *F. candida*), and four species cultured from specimens obtained from the field sites: **Field** *F. candida*, *Tullbergia krausbaueri* (BÖRNER), *Proisotoma minuta* (TULLBERG) and *Isotoma notabilis* SCHÄFFER. Both **Lab.** and **Field** *F. candida* were examined to test any effects of continuous culturing on this species, and since parthenogenesis has been found in several species of Collembola the possibility of parthenogenesis occurring in any of these species was investigated.

The fecundity and mortality of **Lab.** and **Field** *F. candida* were measured at a range of *p*H's at 20 °C, and a range of temperatures at *p*H's 7.6, 5.2 and 2.5. The fecundity and mortality of *T. krausbaueri*, *P. minuta* and *I. notabilis* were assessed at a range of *p*H's at 20 °C. The effect of salinity on **Lab.** *F. candida* was tested at 20 °C with culture media of *p*H 5.2.

2. Materials and methods

In a preliminary experiment with **Lab.** *F. candida* (HUTSON 1978) fecundity differed between *p*H's 5.2 and 4.3. In experiments described here, the effect of *p*H on collembolan fecundity and mortality was investigated in greater detail by examining the effects of an extended range of *p*H's (2.5—7.6 at approximately one *p*H unit intervals) made available by the plaster-charcoal method of substrate preparation previously described (HUTSON 1978), using charcoals of differing *p*H values.

It was also established in the preliminary experiment that at 0 and 30 °C no oviposition occurred, and at 5 °C much time was required to obtain results; for these experiments, therefore, the effect of temperature was examined only at 10, 15, 20 and 25 °C.

Salinity effects were examined by making up cultures of *p*H 5.2 and allowing them to dry completely. After brushing the surface, sodium chloride solutions at seven concentrations were added to the plaster-charcoal substrate to saturation point. The solutions were prepared by dissolving Analar NaCl in triple distilled water in quantities given by RICHARDS (1954: Table 1). Distilled water, not salt solution, was added when required to maintain a high humidity so that the culture solutions were not concentrated further.

Table 1. Concentrations of sodium chloride required for different salinity levels at 25 °C (from RICHARDS 1954)

Conductivity ($mS \cdot cm^{-1}$)	NaCl (gm/100 cc H_2O)
0	0.00
1	0.05
2	0.10
4	0.21
8	0.43
16	0.90
32	1.95

Note. — $1\ S/m = 1\ \Omega \cdot m = 1\ m^{-3} \cdot kg^{-1} \cdot S^3 \cdot A^2$

The small variation in the number of eggs produced per culture in the preliminary experiment indicated that few replicates would be required for these experiments, and for the purpose of statistical comparisons, five replicates of each treatment were used. Two rather than twenty individuals per culture unit (plastic pots with 19.6 cm^2 floor area) were chosen, not only because the smaller numbers of eggs laid and juveniles hatching in the two-individual cultures were more practicable to count but also because of the reduced fecundity using twenty individuals (HUTSON 1978).

More than five cultures of each treatment were prepared, and two individuals of each species (or kind of *F. candida*), small enough not to have previously oviposited, were introduced into each culture. The food and conditions (a mixture of brewer's yeast and potato dextrose agar) were the same as in the preliminary experiment (HUTSON 1978). It was not known whether the cultures

contained two males, two females or one of each sex. They were therefore examined daily, and the first five of each treatment to produce eggs were used in the experiment. For extreme conditions of *p*H and salinity where no oviposition occurred, five cultures were chosen arbitrarily to determine mortality. When oviposition had commenced, the cultures were examined once every two days, or at least three times per week. Egg developmental time was calculated from the day of oviposition to when 50 % of the eggs in a single batch had hatched.

The possibility of parthenogenesis occurring in any of the five kinds of Collembola was investigated by culturing 10 eggs from each species (or kind) separately at 20 °C, *p*H 5.2 and observing the fecundity of the individuals (males and unfertilized females) that hatched.

The significant difference between results for fecundity and mortality at the various temperatures, *p*H's and salinity levels was tested by analysis of variance. For analysis of eggs per culture and eggs per batch only treatments which produced eggs were compared. Since no significant differences were found between the 95 % confidence limits of replicate mean numbers of eggs per batch, the results at each treatment were pooled and only the treatment mean square was used to compare with the residual mean square. The individual 95 % confidence limits **(C.L.)** around each treatment mean were calculated from each treatment sum of squares.

3. Results

3.1. Parthenogenesis

Although three eggs of *I. notabilis* did not hatch, all other eggs of this and the remaining species hatched and juveniles developed normally. **Lab.** *F. candida* began to oviposit after a mean of 18.5 days from hatching, and all individuals laid eggs. Over a period of 73 days, they produced a mean of 68 eggs each. No eggs were produced by any other isolated individuals including **Field** *F. candida*.

From these results, it appeared that the **Lab.** *F. candida* culture consisted entirely of parthenogenetic females, whereas the four other groups could not reproduce parthenogenetically and males were required for fertilization.

3.2. Temperature

Fecundity and mortality data for **Lab.** and **Field** *F. candida* at *p*H 5.2 for the four temperatures examined are summarised in Table 2. The **Lab.** *F. candida* cultures contained two parthenogenetic individuals; since it was not known how many eggs each individual had laid, the mean (and C.L.) of the number of eggs laid by two females is given.

The numbers of eggs per culture produced by **Lab.** and **Field** *F. candida* differed significantly between temperatures ($P < 0.001$ and $P < 0.05$ respectively). Oviposition was greatest at 15 °C (max. 230) for **Lab.** *F. candida* and at 15 and 20 °C (max. 80 and 83) for **Field** *F. candida*. The numbers of eggs per batch also differed significantly between temperatures ($P < 0.05$) with larger batches produced at 15 and 20 °C (max. 89 at 15 °C for **Lab.** *F. candida* and 42 at 20 °C for **Field** *F. candida*). The parent survival time at 10, 15 and 20 °C was very long for both types of this species (>400 days) and final figures are only available for 25 °C (Table 2), where survival was significantly less than 400 days.

A relationship was found between the reciprocal of egg developmental time (days) and temperature (°C) for *F. candida* at the five temperatures examined (Fig. 1). The results for 5 °C were obtained during the preliminary experiment (Hutson 1978). Extrapolation of the graph shows a developmental "zero" at about 3.5 °C, and using this figure, the thermal constants at 25, 20, 15, 10 and 5 °C are 183, 188, 195, 201 and 204 day degrees respectively. Thus, the thermal constant is close to 190 day degrees at all temperatures but shows a gradual increase with reduction of the culture temperature, indicating some non-linearity.

3.3. *p*H

Fecundity and mortality data for Collembola cultured at 20 °C at seven *p*H values are summarised in the following tables: **Lab.** and **Field** *F. candida* (Table 3), *T. krausbaueri* (Table 4), *P. minuta* (Table 5) and *I. notabilis* (Table 6). Again, for **Lab.** *F. candida*, the mean (and C.L.) of the numbers of eggs laid by two females are presented.

Table 2. Fecundity and longevity of **Lab.** and **Field** *Folsomia candida* at different temperatures (*p*H 5.2, **Lab.** *F. c.* 2 females, **Field** *F. c.* 1 female)

Temp. °C		No. of days to 1st oviposition			Duration of oviposition (days)			No. of eggs laid by 2 females (L) or 1 female (F)			No. of eggs per batch			% of eggs hatching	Embryonic develop time (days)	"Parent" survival time (days)		
		Mean	Max.	Min.	Mean	Max.	Min.	Mean ±S.E.	CL*) −	+	Mean ±S.E.	CL −	+	Mean	Mean	Mean ±S.E.	CL −	+
25	L	4.2	5	4	6.4	7	4	118.2 ±8.1	95.7	140.7	29.6 ±3.5	22.2	37.0	*97.5*	8.5	126.3 ±7.8	108.6	144.0
	F	11.7	14	11	2.0	2	2	27.6 ±4.3	15.7	39.5	23.0 ±2.5	16.5	29.5	*95.7*	8.2	85.7 ±12.0	58.5	112.9
20	L	6.8	8	6	16.8	24	12	141.6 ±8.8	117.2	166.0	37.3 ±4.4	28.4	47.0	*97.0*	11.4	>400	—	—
	F	12.8	16	11	8.6	17	2	60.0 ±5.4	45.1	74.9	25.0 ±2.2	20.2	29.8	*91.6*	11.0	>400	—	—
15	L	9.8	13	9	17.2	28	5	200.5 ±13.1	164.1	236.9	37.1 ±3.7	29.5	44.7	*98.8*	17.0	>400	—	—
	F	25.5	29	19	25.2	51	2	64.0 ±8.1	41.6	86.4	24.6 ±1.6	21.2	28.0	*94.3*	17.4	>400	—	—
10	L	16.4	18	16	18.4	38	6	107.6 ±15.9	63.5	151.7	24.4 ±1.6	21.1	27.7	*98.2*	32.0	>400	—	—
	F	27.0	36	9	33.2	47	15	58.6 ±10.0	30.9	86.3	18.3 ±1.7	14.7	21.9	*93.8*	31.4	>400	—	—

*) CL = 95 % confidence limits.

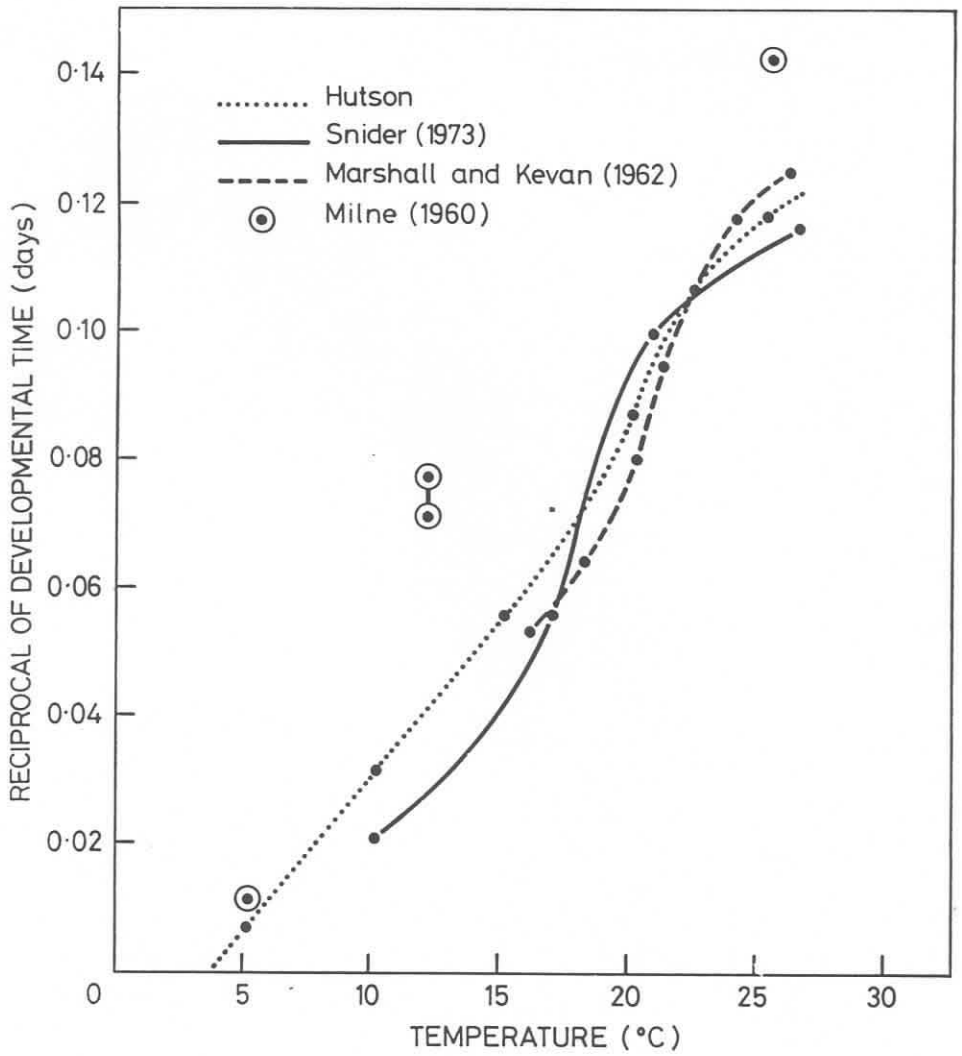

Fig. 1. Relationship between temperature and egg developmental time for *Folsomia candida*.

It was found difficult to culture *I. notabilis* under any *p*H and temperature conditions and the very low survival time, although longer at *p*H 5.2 to 7.2, suggests that the culture method used was not satisfactory for this species. Eggs were only produced at *p*H 5.2 and 6.2, in relatively low numbers (max. 20 per female and 13 per batch), and the percentage hatching was low. The results of a simple t-test showed no significant difference between the numbers of eggs per culture or per batch at these *p*H, and the C.L. also showed no difference.

No eggs were produced by any species at *p*H 2.5, some eggs were laid by **Lab.** *F. candida* and *T. krausbaueri* at *p*H 3.3, and *T. krausbaueri* was the only species to oviposit at *p*H 7.6.

The numbers of eggs per culture for all species (or types) except *I. notabilis* differed significantly between *p*H ($P < 0.001$). Oviposition was greatest at *p*H 5.2 for **Lab.** *F. candida* (max. 166 per parthenogenetic pair), **Field** *F. candida* (max. 87) and *T. krausbaueri* (max. 67). For *P. minuta*, however, greatest oviposition was at *p*H 7.2 (max. 48).

The numbers of eggs per batch followed a similar trend and batches produced by both **Lab.** and **Field** *F. candida* and *T. krausbaueri* differed significantly between *p*H ($P < 0.01$ and $P < 0.001$ respectively). The mean batch sizes were greatest at *p*H 5.2 with maxima at *p*H 5.2 for **Lab.** *F. candida* (max. 85) and *T. krausbaueri* (max. 23), and at *p*H 6.2 for **Field** *F. candida* (max. 44). For *P. minuta*, the numbers of eggs per batch did not differ significantly but the C.L. showed batch sizes at *p*H 7.2 (max. 21) to be greater than at *p*H 4.3, 5.2 and 6.2.

Table 3. Fecundity and longevity of **Lab.** and **Field** *Folsomia candida* at different *p*H's (20 °C; **Lab.** *F. c.* 2 females, **Field** *F. c.* 1 female)

*p*H		No. of days to 1st oviposition			Duration of oviposition (days)			No. of eggs laid by 2 females (L) or 1 female (F)			No. of eggs per batch			% of eggs hatching	Embryonic develop. time (days)	"Parent" survival time (days)		
		Mean	Max.	Min.	Mean	Max.	Min.	Mean ±S.E.	CL −	CL +	Mean ±S.E.	CL −	CL +	Mean	Mean	Mean ±S.E.	CL −	CL +
7.6	L	—	—	—	—	—	—	0	—	—	—	—	—	—	—	157.5 ±8.1	139.2	175.8
	F	—	—	—	—	—	—	0	—	—	—	—	—	—	—	121.8 ±15.1	87.7	155.9
7.2	L	7.0	8	6	8.7	17	2	58.8 ±3.3	49.7	67.9	18.4 ±2.1	13.9	22.9	*55.7*	11.0	186.4 ±7.1	170.4	202.6
	F	6.0	7	5	2.0	2	2	4.0 ±1.0	1.2	6.8	4.0 ±1.0	1.2	6.8	*0.0*	—	170.5 ±20.1	125.1	215.9
6.2	L	6.4	8	4	4.8	12	2	64.4 ±8.6	40.6	88.2	20.1 ±3.9	11.7	28.5	*97.8*	11.6	>400	—	—
	F	12.7	16	11	16.2	30	3	52.0 ±7.9	30.0	74.0	23.6 ±3.0	16.8	30.4	*78.0*	11.4	>400	—	—
5.2	L	6.8	8	6	16.8	24	12	141.6 ±8.8	117.2	166.0	37.3 ±4.4	28.0	46.6	*97.0*	11.4	>400	—	—
	F	12.8	16	11	8.6	17	2	60.0 ±5.4	45.1	74.9	25.0 ±2.2	20.2	29.8	*91.6*	11.0	>400	—	—
4.3	L	7.6	9	6	12.2	14	10	93.2 ±10.2	65.0	121.4	27.4 ±3.8	19.3	35.5	*88.4*	11.2	240.5 ±24.9	184.2	296.8
	F	11.4	14	9	6.0	14	2	48.8 ±6.0	32.2	65.4	24.4 ±3.3	17.0	31.8	*80.0*	11.0	114.2 ±25.3	56.9	171.5
3.3	L	8.7	11	6	4.0	10	1	13.4 ±1.8	8.4	18.4	13.4 ±1.8	8.4	18.4	*0.0*	—	48.8 ±2.0	44.2	53.6
	F	—	—	—	—	—	—	0	—	—	—	—	—	—	—	30.8 ±1.8	26.7	34.9
2.5	L	—	—	—	—	—	—	0	—	—	—	—	—	—	—	20.9 ±1.4	17.8	24.0
	F	—	—	—	—	—	—	0	—	—	—	—	—	—	—	19.9 ±2.7	13.9	25.9

Table 4. Fecundity and longevity of *Tullbergia krausbaueri* at different *p*H's (20 °C, 1 female)

*p*H	No. of days to 1st oviposition			Duration of oviposition (days)			No. of eggs laid by 1 female			No. of eggs per batch			% of eggs hatching	Embryonic develop. time (days)	"Parent" survival time (days)		
	Mean	Max.	Min.	Mean	Max.	Min.	Mean ±S.E.	CL −	+	Mean ±S.E.	CL −	+	Mean	Mean	Mean ±S.E.	CL −	+
7.6	11.0	18	4	3.7	7	2	4.6 ±1.2	1.2	8.0	2.3 ±0.3	1.6	3.0	*0.0*	—	153.2 ±17.5	113.5	192.9
7.2	15.8	23	11	7.0	19	2	6.6 ±1.2	3.2	10.0	3.3 ±0.4	2.5	4.1	*0.0*	—	140.8 ±17.7	100.8	180.8
6.2	12.2	18	9	44.6	41	32	29.8 ±4.5	17.4	42.2	6.2 ±0.9	4.4	8.0	*94.0*	23.2	>400	—	—
5.2	8.2	11	6	44.2	44	41	52.0 ±4.7	38.6	65.0	11.8 ±1.0	9.7	13.9	*95.5*	24.4	>400	—	—
4.3	13.4	25	6	22.2	33	16	25.2 ±2.2	19.1	31.3	6.0 ±0.7	4.5	7.5	*94.0*	24.0	>400	—	—
3.3	5.4	8	4	4.8	12	2	5.2 ±1.9	0.0	10.4	3.2 ±0.5	2.0	4.4	*0.0*	—	39.8 ±6.3	25.6	54.0
2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8.9 ±0.8	7.1	10.7

Table 5. Fecundity and longevity of *Proisotoma minuta* at different *p*H (20 °C, 1 female)

*p*H	No. of days to 1st oviposition			Duration of oviposition (days)			No. of eggs laid by 1 female			No. of eggs per batch			% of eggs hatching	Embryonic develop. time (days)	"Parent" survival time (days)		
	Mean	Max.	Min.	Mean	Max.	Min.	Mean ±S.E.	CL −	+	Mean ±S.E.	CL −	+	Mean	Mean	Mean ±S.E.	CL −	+
7.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	149.8 ±25.2	92.9	206.7
7.2	11.2	18	9	17.2	29	8	42.0 ±2.5	35.0	49.0	21.0 ±2.0	16.4	25.6	*95.5*	8.5	143.4 ±18.5	101.6	185.2
6.2	12.5	16	9	6.5	9	4	21.6 ±1.0	18.8	24.4	10.8 ±1.0	8.4	13.2	*77.0*	8.6	114.3 ±20.3	68.3	160.3
5.2	9.0	10	8	12.5	14	9	20.8 ±2.7	13.3	28.3	13.0 ±1.6	9.2	16.8	*94.0*	8.8	157.5 ±17.8	117.2	197.8
4.3	14.0	16	11	11.0	15	8	16.6 ±4.3	4.7	28.5	10.8 ±1.9	6.1	15.5	*97.0*	8.5	123.7 ±16.1	87.4	160.0
3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19.5 ±2.0	15.0	24.0
2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19.8 ±2.4	14.4	25.2

Table 6. Fecundity and longevity of *Isotoma notabilis* at different *p*H (20 °C, 1 female)

*p*H	No. of days to 1st oviposition			Duration of oviposition (days)			No. of eggs laid by 1 female			No. of eggs per batch			% of eggs hatching	Embryonic develop. time (days)	"Parent" survival time (days)		
	Mean	Max.	Min.	Mean	Max.	Min.	Mean ±S.E.	CL —	+	Mean ±S.E.	CL —	+	Mean	Mean	Mean ±S.E.	CL —	+
7.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23.3 ±3.4	15.6	31.0
7.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	44.8 ±10.7	20.6	69.0
6.2	12.0	16	4	8.0	16	2	13.0 ±1,8	8.0	18.0	5.4 ±0,8	3.6	7.2	*15.0*	9.7	56.6 ±7.3	40.1	73.1
5.2	19.2	23	13	8.0	17	2	15.2 ±1.8	10.1	20.3	6.9 ±0.8	5.1	8.7	*13.0*	10.0	83.4 ±14.5	50.4	116.4
4.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18.7 ±3.6	10.6	26.8
3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13.7 ±1.9	9.4	18.0
2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9.2 ±1.4	5.9	12.5

The percentage hatch at *p*H 4.3, 5.2 and 6.2 was high for all species (or types) except *I. notabilis*. A high percentage hatch was also recorded at *p*H 7.2 for *P. minuta;* the lower figure for this species at *p*H 6.2 was due to mould on the eggs in two of the cultures. Although some eggs were laid by both types of *F. candida* at *p*H 7.2, the hatching percentage of **Lab.** *F. candida* was greatly reduced and no **Field** *F. candida* eggs hatched. Eggs laid by **Lab.** *F. candida* and *T. krausbaueri* at *p*H 3.3 also did not hatch and no hatching occurred from eggs laid by **Field** *F. candida* and *T. krausbaueri* at *p*H 7.2 or 7.6.

Parent survival time for **Lab.** and **Field** *F. candida* was greatest (> 400 days) at *p*H 5.2 and 6.2, and at *p*H's 4.3, 5.2 and 6.2 for *T. krausbaueri.* Survival time was least at the lower *p*H; where no oviposition occurred at the higher *p*H, survival time was not reduced to the same extent. *P. minuta* and *I. notabilis* did not survive as long as *F. candida* and *T. krausbaueri* and final results, obtained from all *p*H levels, differed significantly between *p*H's ($P < 0.001$). The maximum survival time for *P. minuta* and *I. notabilis* was 291 days at *p*H7.6 and 190 days at *p*H 5.2 respectively.

Table 7 shows the effect of extremes of *p*H (7.6 and 2.5) on the survival rate of **Lab.** and **Field** *F. candida* at four temperatures.

At lower temperatures the survival time increased, but final results (> 400 days) are not available for the lower temperatures at *p*H 7.6. The survival time at *p*H 2.5, however, was short (max. 55 and 54 days at 10 °C for **Lab.** and **Field** *F. candida* respectively) and differed significantly between temperatures ($P < 0.01$ and $P < 0.001$ respectively).

3.4. Salinity

Fecundity and mortality data for **Lab.** *F. candida* at *p*H 5.2 and 20 °C for the seven salinity levels examined, are given in Table 8. With increasing salinity, the number of days before oviposition commenced tended to increase and the duration of oviposition decreased. Most eggs were produced at conductivity 0 $mS \cdot cm^{-1}$ (max. 100 per culture) and least at 16, with no eggs produced at conductivity 32. The differences were significant ($P < 0.001$) but the reduction of egg production at higher salinities only became significant above con-

Table 7. Longevity of **Lab.** and **Field** *Folsomia candida* at different temperatures at *p*H 7.6 and 2.5

*p*H	Temp. °C	No. of eggs laid by 2 females (**L**) or 1 female (**F**)	"Parent" survival time (days) Lab. F.c.			Field F.c.		
			Mean ± S.E.	CL −	+	Mean ± S.E.	CL −	+
7.6	25	0	128.9 ±8.4	110.0	147.8	93.5 ±8.4	74.5	112.5
	20	0	157.5 ±8.1	139.2	175.8	121.8 ±15.1	87.7	155.9
	15	0	>400	—	—	>400	—	—
	10	0	>400	—	—	>400	—	—
2.5	25	0	14.6 ±1.5	11.1	18.1	17.9 ±2.5	12.3	23.5
	20	0	20.9 ±1.4	17.8	24.0	19.9 ±2.7	13.9	25.9
	15	0	23.6 ±3.4	15.9	31.3	26.5 ±3.8	18.0	35.0
	10	0	31.9 ±4.5	21.8	42.0	37.2 ±2.5	31.6	42.8

Table 8. Fecundity and longevity of **Lab.** *Folsomia candida* at different salinity levels (20 °C, *p*H 5.2, 2 females)

Conductivity mS · cm^{-1}	No. of days to 1st oviposition			Duration of oviposition (days)			No. of eggs laid by 2 females			No. of eggs per batch			% of eggs hatching	Embryonic develop. time (days)	"Parent" survival time (days)		
	Mean	Max.	Min	Mean	Max.	Min.	Mean ±S.E.	CL −	CL +	Mean ±S.E.	CL −	CL +	Mean	Mean	Mean ±S.E.	CL −	CL +
0	5.4	7	4	19.0	34	9	90.8 ±3.2	81.8	99.8	28.4 ±2.3	23.6	33.2	*99.0*	11.0	>400	—	—
1	6.2	8	4	15.8	26	9	70.6 ±4.0	59.6	81.6	25.2 ±2.7	19.4	31.0	*98.4*	11.0	>400	—	—
2	5.8	9	4	16.8	24	9	85.8 ±3.2	77.2	94.8	25.2 ±2.1	20.8	29.6	*95.4*	11.8	>400	—	—
4	7.0	7	7	10.8	14	4	69.6 ±4.5	57.1	82.1	24.8 ±2.5	19.4	30.2	*98.5*	11.8	>400	—	
8	8.2	9	7	10.4	19	4	75.0 ±5.3	60.4	89.6	28.8 ±2.9	22.4	35.2	*91.7*	11.0	>400	—	—
16	10.4	11	9	3.6	5	2	44.6 ±5.9	28.2	61.0	18.6 ±1.7	14.9	22.3	*10.9*	11.0	>400	—	—
32	—	—	—	—	—	—	—	—	—	—	—	—	—	—	92.5 ±22.6	51.1	133.9 ±33.9

ductivity 8. The numbers of eggs per batch (max. 46 at conductivity 8) did not differ significantly between salinity levels; only the C.L. of conductivities 0 and 8 compared with 16 were significantly different. The percentage hatching was high up to conductivity 8, but was much less at 16. Many of the eggs produced at 16 were very deformed; often groups of two or three eggs were small and fused together, and of those juveniles which did hatch, only three lived for more than two days and then did not moult or develop.

Up to conductivity 8, parent survival time was not apparently affected although final results are not available. Although adults survived for more than 400 days at conductivity 16, after 40 days individuals were thinner and less agile than at lower conductivities. At conductivity 32, two individuals died at 4 and 7 days, and although the remainder were alive for up to 136 days. they were reduced to about half their original size for most of that time, and were completely motionless except for antennal movements; it was assumed that they did not eat.

4. Discussion

A summary of some published data on the life history of *F. candida*, a species which has often been studied, is given in Table 9. Comparison of these data with the results presented here, shows large discrepancies between the fecundities obtained at similar temperatures.

Green (1964a) suggests that the difference between his results and those of Milne (1960) may have been due to **(a)** Green's use of solitary cultures, **(b)** a temperature difference of 1 °C, **(c)** his use of a different food (yeast instead of bracken spores) and **(d)** a difference in genetic strains. Populations used by Snider (1973), Snider and Butcher (1973), Green (1964a) and Marshall and Kevan (1962) were entirely parthenogenetic whilst it is probable that sexual reproduction occurred in the populations used by Milne (1960).

Table 9. Comparison of data on *Folsomia candida* obtained by various authors (adapted from Snider 1973)

Temp. °C	Author	Embryonic devel. time (days)	% hatching	No. of eggs produced in lifetime	No. of eggs per batch
28.0	M + K	7— 8*)	*81.7*	—	—
26.6	S	8— 9	*90.2*	—	—
26.0	S + B	—	—	209 Maximum	—
26.0	M + K	7— 9 (8.2)	*75.0*	—	—
25.0	G	5—15 (7.0)	—	(167.5)	29—61
25.0	H1	8— 9 (8.5)	*97.5*	(59.1)	8—61
24.0	M + K	7—10 (9.2)	*88.9*	19—62 (39.6)	3—20 (yeast diet)
24.0	M + K	—	—	—	14—29 (leaf diet)
24.0	M	7— 9	—	(30.0)	9—36
22.0	M + K	9—10	*87.8*	—	—
21.0	S	9—11	*94.7*	128—1654 (1011)	2—157
20.0	H1	11—12 (11.4)	*97.0*	(70.8)	8—85
20.0	M + K	10—15 (14.8)	*71.5*	—	—
18.0	M + K	15—16	*46.7*	—	—
16.0	M + K	18—20	*52.0*	—	—
15.5	S	17—20	*87.1*	—	—
15.0	S + B	—	—	2355 Maximum	—
15.0	H1	16—18 (17.0)	*98.8*	(100.2)	3—89
12.0	M	13—15	—	(22.0)	—
10.0	S	40—45	*11.6*	—	—
10.0	H1	30—34 (32.0)	*98.2*	(53.8)	12—32
5.0	M	90	—	(29.0)	—
5.0	H2	134—138 (136.0)	*53.0*	(48.0)	5—35

Note. — (M + K) Marshall and Kevan (1962); (S) Snider (1973); (S + B) Snider and Butcher (1973); (G) Green (1964a); (M) Milne (1960); (H1) Present study, *p*H 5.2; (H2) Hutson (1978), *p*H 5.2. Figures in parenthesis = mean figures. *) eggs laid by females previously kept at 28 °C.

In the experiments described here, **Lab.** *F. candida* were found to be parthenogenetic, whereas no evidence of this was found in the **Field** *F. candida*. Only one individual in each **Field** *F. candida* culture was seen to be gravid and the other individual of each pair was assumed to be male. This is supported by the work of GOTO (1960b) who found that wild populations of *F. candida* in England contain males and females in approximately equal numbers. The mean numbers of eggs in the **Field** *F. candida* cultures were much less than half the numbers of eggs produced by the two females in the **Lab.** *F. candida* cultures at all temperatures except 10 °C, and the numbers of eggs per batch were also less (Table 2). Also, although eggs were laid by **Field** *F. candida* at *p*H 7.2, many more were laid by **Lab.** *F. candida*, and at *p*H 3.3 only **Lab.** *F. candida* produced any eggs at all. Thus, there do seem to be physiological differences between the genetic strains.

GREEN (1964a) also points out that the limited reproductive period observed in the laboratory would probably not be found in field situations since the life of the animals in culture extended to more than three times the period from hatching to the end of oviposition. This view is supported by SNIDER (1973) who obtained a mean of 1011 eggs per female *F. candida* at 21 °C, and one female kept at 15 °C produced 2355 eggs (SNIDER and BUTCHER 1973); these figures are far greater than any others published. SNIDER (1973) also found that the maximum longevity at 21 °C was 198 days, death occurring at a mean of one instar (maximum eight days) after oviposition had ceased. *F. candida* was found to survive for up to 230 days at 25 °C by GREEN (1964a), but only 111 days at 24 °C by MARSHALL and KEVAN (1962). The greatest fecundity in this work was a mean of 175 eggs per female at *p*H 5.2, 20 °C during a preliminary experiment (HUTSON 1978) but under the same conditions, as well as at lower temperatures, during the experiments described here, parents survived for longer than 400 days, only a small proportion of which was spent ovipositing. GREEN (1964a) found eggs in the ovaries on post-mortem examinations and assumed that some inhibitory factor operated after a period of time in the cultures. He also found that *F. candida* can condition an area to attract other individuals and suggests that an accumulation of these secretions might inhibit oviposition or development of the ovaries (GREEN 1964b). Similarly, accumulation of excretory products might contaminate the surface of cultures and inhibit oviposition. CHRISTIANSEN (1967), using several species of Collembola, found a depression of reproduction in mass cultures after 200—300 days. SNIDER (1973) transferred her experimental animals to fresh cultures whenever the substrate became badly contaminated (generally after 60—70 days and again after 140 days). Although cultures were never seen to be "badly contaminated" during the experiments described here, and were therefore never changed, this factor may have contributed to the overall reduced fecundity at optimum *p*H and temperature conditions.

Apart from the addition of results at 15 °C, the fecundity variations of the **Lab.** *F. candida* in this experiment were similar to those obtained in a preliminary experiment (HUTSON 1978) except that lower total numbers of eggs were produced at 25, 20 and 10 °C. Although the preliminary results were based on only two replicates, both results were higher than any of the five replicate results in these experiments (except one culture at 10 °C), and the duration of oviposition was longer. This may have been caused by the selection of animals at different times from different mass cultures. Those used in the preliminary experiment were taken from a culture separated from the original stock culture and re-housed six months earlier whereas those taken for these experiments were all from the original stock culture. GREEN (1964b) found that reducing the density of overcrowded cultured increased fecundity. He found no long term effect on the fecundity of one generation whilst individuals were still able to oviposit, but the fecundity of individuals taken from the original culture may have been affected by overcrowding and contaminated conditions for several generations. One year after the start of the experiment, the original culture was rapidly dying out and could be seen to be heavily contaminated with waste products whereas individuals in the re-housed culture appeared to have recovered.

Until now, other authors have assumed that the method of preparing the plaster-charcoal substrate has no effect on the animals. There is generally no description of the type of

charcoal used except by GOTO (1960a), CHOUDHURI (1960) and VAIL (1965) who state that activated charcoal was used; the ratio of plaster to charcoal also varies between authors. The results here (based on the method of substrate preparation described by HUTSON (1978) using various ratios of activated: animal charcoal) show that the type of charcoal used can have a profound effect on the fecundity and longevity of collembolan species, and that this effect is caused by the change in *p*H of the culture medium. At low *p*H's, the effect is probably direct since death was relatively rapid and little (if any) feeding took place. At more habitable *p*H's, however, an indirect effect may contribute to variation. Substrate *p*H can have a great effect on the population of adventitious bacteria and fungi. In culture, this may cause variation in food utilised and it has been shown that the type and quality of diet can influence collembolan growth and fecundity (SNIDER 1971).

Compared with other authors, a lower ratio of plaster to charcoal (1: 4) was used in this work in order to obtain the various *p*H conditions, and it is suggested that the discrepancies between results reported by different authors could have been caused in part by such chemical differences in their cultures. Under field conditions, it is expected that fecundity will be affected by *p*H, but the effect will not necessarily be the same as in the laboratory cultures since there are many other environmental factors also affecting fecundity in the field.

A linear relationship between the reciprocal of egg developmental time and temperature similar to that obtained for *F. candida* was found by HALE (1965b) for several species from each family of Collembola. The results given by MARSHALL and KEVAN (1962) and SNIDER (1973) when transformed and plotted graphically (Fig. 1) are very similar to the results obtained here; there seems to be a straight line relationship at low temperatures, but a slight curve at higher temperatures. The three figures for *F. candida* given by MILNE (1960) differ greatly from these results especially at the higher temperatures.

According to MARSHALL and KEVAN (1962), the optimum temperature for hatching of *F. candida* eggs is 22—24 °C, which gave about 90 % hatch of eggs laid at 24 °C; only about 75 % hatched at 20 and 26 °C and about 50 % at 16 and 18 °C. SNIDER (1973), using eggs laid at 21 °C, found the optimum temperature to be 21 °C (94.7 % hatch) and 26.6 °C (90.2 % hatch) whilst at 15 and 10 °C, 87.1 and 11.6 % hatched. In the work presented here, however there was no difference between the hatching percentage for **Lab.** and **Field** *F. candida* at 25, 20, 15 or 10 °C; all eggs were laid at culture temperature. CHOUDHURI (1963) states that the percentage of eggs completing development successfully depends partially on temperature, but he could find no significant difference within a wide range of temperatures for three species of *Onychiurus*. Some of the figures published for *F. candida* may not be related to field conditions since with decreasing temperature there is an increase in developmental time and some eggs may be spoiled in the culture. In the field, however, the longer the developmental time of the egg, the more likely it is to be eaten by predators, or to be damaged by physical disturbance of the soil.

Only effects of *p*H and the possibility of parthenogenetic reproduction were examined using *T. krausbaueri*, *P. minuta* and *I. notabilis*, and there is little published work for comparison. Tables 10 and 11 summarise the fecundity data previously available for *T. krausbaueri* and *I. notabilis*. The *p*H of the culture again had a great effect on fecundity and longevity, and a *p*H of about 5.2 was shown to be the optimum for *T. krausbaueri* and *I. notabilis*, and of about 7.2 for *P. minuta*. The thermal constant for *T. krausbaueri* given by HALE (1965c) was used to estimate the egg development time at various temperatures and the figure of 26 days at 20 °C compares closely with the results obtained here (about 24 days). The figure given by MILNE (1960) for *T. krausbaueri* eggs at 12 °C (15—20 days) appears to be rather low in comparison, as were the figures for numbers of eggs per female and per batch. HALE (1965b) estimated that one female could produce 55 eggs in a lifetime and this figure is supported by the results here at *p*H 5.2 (52 eggs per female). HALE found a mean of 5.5 eggs per batch at 15 °C, but at 20 °C, *p*H 5.2, a mean of 11.0 eggs per batch was found in these experiments. SHARMA and KEVAN (1963a) found a mean of 47 eggs per female *I. notabilis* at 17 °C, but the figures presented here are unreliable since this species was so difficult to culture.

Table 10. Comparison of data on *Tullbergia krausbaueri* given by MILNE (1960) and HALE (1965b)

Temperature °C	Author	Embryonic develop. time (days)	No. of eggs produced in lifetime	No. of eggs per batch
20	Present study+)	24	52	5—23
20	HALE (1965b)*)	26	—	—
16	HALE (1965b)*)	32	—	—
15	HALE (1965b)*)	34	55	5.5 (±0.3)
12	MILNE (1960)	15—20	10	1—2
10	HALE (1965b)*)	51	—	—
7	HALE (1965b)*)	73	—	—
4	HALE (1965b)*)	128	—	—

+) *p*H 5.2.
*) Estimate from thermal constant figure

Table 11. Data on *Isotoma notabilis* (from SHARMA and KEVAN 1963a)

Temperature	Embryonic develop. time (days)	% hatching	No. of eggs produced in lifetime	No. of eggs per batch
20*)	(10.0)	*13.0*	15.2	2—11
17	7— 8 (7.4)	*87.0*	47.2	7— 8
14	10—12 (10.5)	*68.0*	23.2	—
11	18—21 (19.0)	—	12.8	—
8	30—32 (30.5)	—	6.6	—
6	35—38 (35.7)	*49.0*	6.4	—
4	51—55 (53.6)	—	3.0	—

Figures in parenthesis = mean figures.
*) Present study, *p*H 5.2.

The survival time of *P. minuta* was less than those of *F. candida* and *T. krausbaueri* and since the egg developmental time is also less at 20 °C a shorter generation time may be found in natural conditions.

PETERSON (1971) found both *T. krausbaueri* and *I. notabilis* to be parthenogenetic in Denmark, although males have been found in some populations of *T. krausbaueri* by other authors. *T. krausbaueri* has also been found to be parthenogenetic in England (HALE 1966), but SHARMA and KEVAN (1963a) found no evidence of parthenogenesis in *I. notabilis* from Quebec, since any eggs laid by unmated females did not hatch. Parthenogenesis was not observed in either of these species or in *P. minuta* from the limited areas studied.

The results of the salinity experiment with **Lab.** *F. candida* show that this species is able to survive and reproduce adequately up to conductivity 8 $mS \cdot cm^{-1}$ (which is moderately saline). This is comparable with results obtained by plant ecologists which show that between conductivity 2—4 (very slightly saline), the yield of sensitive crops may be reduced, and between conductivity 4—8, the yield of many crops is restricted. During the survey of reclamation sites (HUTSON 1974) salinity levels were never even moderately saline, so that salinity would not have been a limiting factor at least for *F. candida*.

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6. Summary . Zusammenfassung

Laboratory culture experiments were carried out with Collembola kept on a substrate of plaster of Paris and charcoal. Parthenogenesis was shown to occur in an old stock culture of *Folsomia candida* (**Lab.** *F. candida*) but not in species collected from the field (**Field** *F. candida*, *Tullbergia krausbaueri*, *Proisotoma minuta* and *Isotoma notabilis*).

The exact composition of the culture substrate affected its *p*H and had a profound effect on the fecundity and longevity of the four species examined. At 20 °C, the optimum *p*H range was generally between 4.3 and 6.2. Fecundity was greatest at *p*H 5.2 for *F. candida* with a mean of 71 eggs per **Lab.** female (maximum 166 per parthenogenetic pair) and 60 per **Field** female (maximum 83), for *T. krausbaueri* with a mean of 52 eggs per female (maximum 67) and for *I. notabilis* with a mean of 15 eggs per female (maximum 20). The fecundity of *P. minuta* was greatest at *p*H 7.2 with a mean of 42 eggs per female (maximum 48). *F. candida* and *T. krausbaueri* survived for more than 400 days under favourable conditions of *p*H, temperature and salinity.

At *p*H 5.2, the fecundity of *F. candida* was greatest at 15 °C with a mean of 100 eggs per **Lab.** female (maximum 230 per parthenogenetic pair) and 64 eggs per **Field** female (maximum 80).

Fecundity and longevity of **Lab.** *F. candida* were not limited by saline conditions up to conductivity 8 mS · cm^{-1}.

Einfluß von pH-Wert, Temperatur und Salzgehalt auf die Fruchtbarkeit und Langlebigkeit von vier Collembolen-Arten

In Laborversuchen wurden Collembolen auf einem Gemisch von Gips und Holzkohle gezüchtet. Parthogenese trat in einem alten Laborzuchtstamm von *Folsomia candida* (**Lab.** *F. candida*), aber nicht bei im Freiland gesammelten Collembolen (**Field** *F. candida*, *Tullbergia krausbaueri*, *Proisotoma minuta* and *Isotoma notabilis*) auf.

Das Mischungsverhältnis des Substrates beeinflußte den *p*H-Wert und hatte einen ausschlaggebenden Einfluß auf die Fruchtbarkeit und Langlebigkeit der vier untersuchten Arten. Bei einer Temperatur von 20 °C lag der optimale *p*H-Wert im allgemeinen zwischen 4.3 und 6.2. Die größte Fruchtbarkeit folgte einem *p*H-Wert von 5.2 bei *F. candida*, die durchschnittlich 71 Eier pro **Lab.**-Weibchen (max. 166 pro parthenogenetischem Paar) und 60 pro **Field**-Weibchen (max. 83) hatte sowie bei *T. krausbaueri* mit durchschnittlich 52 Eiern pro Weibchen (max. 67) und bei *I. notabilis* mit durchschnittlich 15 Eiern pro Weibchen (max. 20). Hingegen zeigte *P. minuta* die größte Fruchtbarkeit bei *p*H 7.2 mit einem Mittel von 42 Eiern pro Weibchen (max. 48). *F. candida* und *T. krausbaueri* überlebten mehr als 400 Tage unter günstigen Bedingungen von *p*H, Temperatur und Salzgehalt.

War das *p*H 5,2, so zeigte *F. candida* die größte Fruchtbarkeit bei 15 °C mit durchschnittlich 100 Eiern pro **Lab.**-Weibchen (max. 230 pro parthenogenetischem Paar) und 64 Eiern pro **Field**-Weibchen (max. 80).

Der Salzgehalt des Substrates hatte bis zu einer Leitfähigkeit von 8 mS · cm^{-1} keinen beschränkenden Einfluß auf Fruchtbarkeit und Lebensdauer von **Lab.** *F. candida*.

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Present address of the author: Dr. Barry R. Hutson, Division of Soils, CSIRO, Private Bag No. 2, P.O. Glen Osmond, S.A. 5064, Australia.